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SOME FLORISTIC RELATIONSHIPS BETWEEN MEXICO AND THE UNITED STATES

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MEXICO has long been recognized as a biological cross-roads between the Americas and as a biotic peninsula in relation to the rest of the continent. It is becoming apparent that the biogeography of North America cannot be properly studied without giving a great deal of attention to its southern extensions and relationships. The floristic similarities between Mexico and the United States, particularly in their eastern regions, were noted by Watson (1891), and this relationship has, in recent years, received notice somewhat proportionate to its biogeographic interest, particularly through Sharp and his collaborators.

Various and somewhat conflicting interpretations have been offered for these floristic relationships. The present, imperfect state of knowledge concerning the eastern Mexican-eastern United States pattern of distribution has been adequately dealt with by Sharp and others (Miranda and Sharp, 1950, Sharp, 1946, 1951). In the present paper, an attempt will be made to review the floristic evidence and to consider in some detail its possible interpretations.

FLORISTIC RELATIONSHIPS

This discussion will largely be limited to the spermatophytes, as these are best known geographically and paleobotanically. Miranda and Sharp (1950) list a number of ferns which occur in eastern Mexico and the eastern United States, as well as some mosses and fungi (see also Sharp, 1948) which show a similar

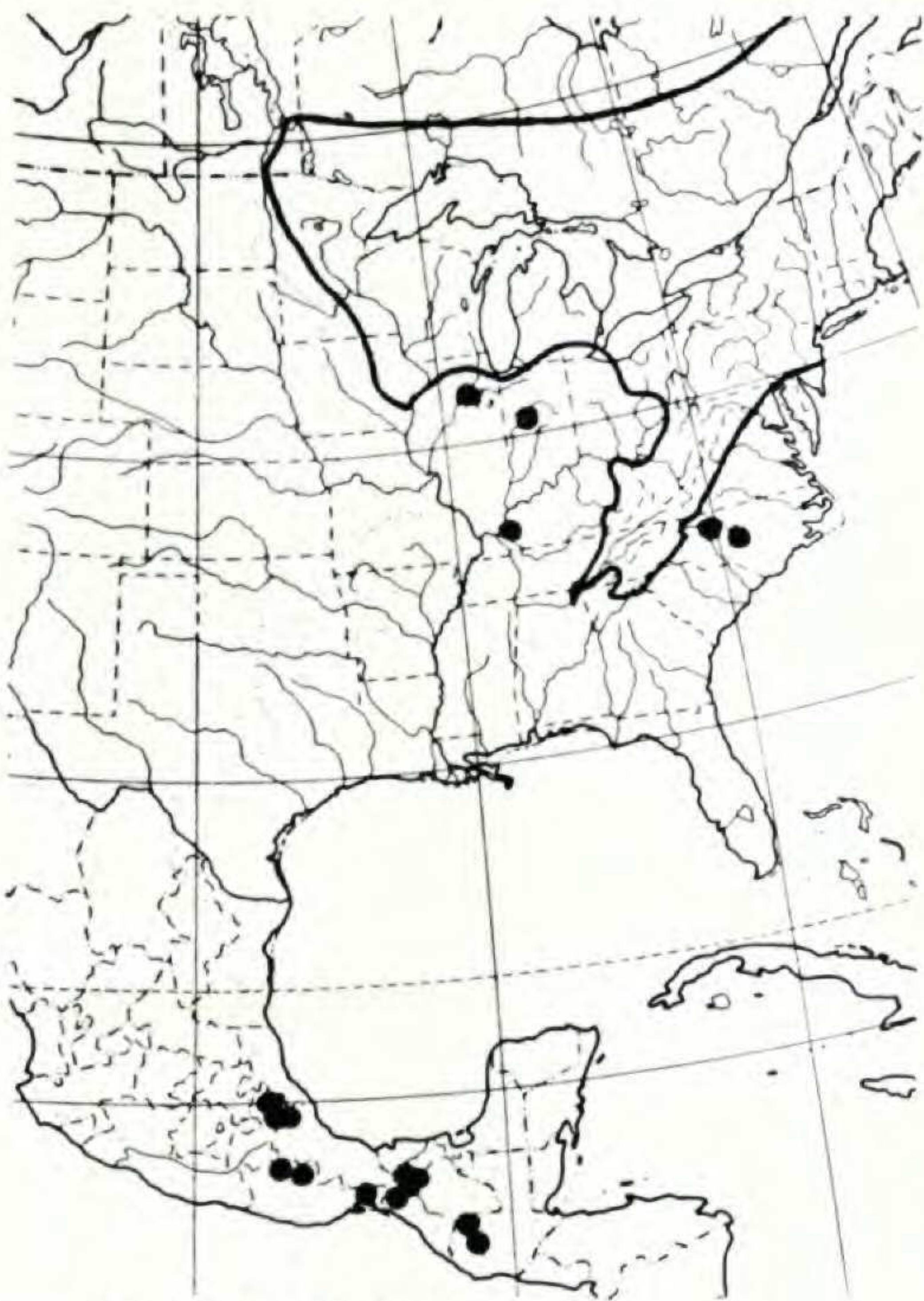
pattern. The characteristic distribution pattern with which this paper is especially concerned is that shown in maps 1 to 6. A number of species that are relatively widespread in the eastern United States occur also on the escarpments of the mountains of eastern and southern Mexico and of Guatemala. Many, if not most, of these plants have disjunct ranges, being absent from southern Texas and northern Mexico and frequently discontinuous in Mexico. Since lists of the species with ranges of this type have been published elsewhere, the present discussion will be limited to species of special interest and a few which have not been listed in the papers cited (Hernández, et al. 1951; Miranda, 1945; Miranda & Sharp, 1950; Sharp, 1946-1952; Steyermark, 1950).

TAXUS GLOBOSA Schlecht.: This species is known from the Mexican states of Veracruz, Hidalgo, Mexico and Oaxaca. Its relationships among the more northern species are uncertain, but it seems to resemble most closely *T. floridana* Nutt., of west Florida.

PINUS STROBUS L. & var. **CHIAPENSIS** Martínez: (Map 1). This species provides one of the most striking distributions of this type. *Pinus Strobus*, which is so generally considered a northern type, has, in recent years, been found to be fairly abundant in the Mexican states of Chiapas, Oaxaca and Puebla and in Guatemala (Martínez, 1945; Sharp, 1946).

PANICUM VILLOSISSIMUM Nash: This grass is widespread in the eastern United States and occurs in Nuevo León, Mexico, but is apparently absent between that station and Guatemala, where other collections of this species have been made (Steyermark, 1950).

EPIDENDRUM CONOPSEUM R. Br. & var. **MEXICANUM** L. O. Wms.: The orchids, with their tiny, wind-blown seeds, are perhaps poor material for phytogeographic study; this species, however, is exceptional among the epiphytic species in its distribution. Other epiphytes of the United States are limited to Florida and are either West Indian or very widespread species. *E. conopseum* is absent from southern Florida and occurs in Alabama and Louisiana and north to southern North Carolina. Its Mexican occurrence, in Morelos, is somewhat west of the usual area for such disjunctions, but the pattern is otherwise



MAP 1. PINUS



MAP 2. TOVARA



MAP 3. ILLICIUM



MAP 4. HAMAMELIS

MAP 1. *Pinus Strobus*. Data from Martínez (1945), Munns (1938) and Sharp (1946). MAP 2. *Tovara virginiana*. Data from Li (1952) and Sharp (1952). MAP 3. *Illicium floridanum* (including *I. mexicanum*). Data from Hernández, et al (1951) and Smith (1947). MAP 4. *Hamamelis virginiana*. Data from Hernández, et al (1951) and Munns (1938).

typical. Its associates in the United States, *Magnolia*, *Liquidambar*, *Fagus*, *Carpinus*, *Acer*, *Taxodium* and *Nyssa* (Correll, 1950), are all trees of typical Mexico-United States disjunct pattern.

TOVARA VIRGINIANA (L.) Raf. (Map 2).

ILLICIUM FLORIDANUM Ellis: (Map 3) The southernmost Mexican collection, from Veracruz, was named *I. mexicanum* by Smith (1947).

LIQUIDAMBAR STYRACIFLUA L.: This tree is abundant in parts of Mexico and occurs as far south as Nicaragua. Miranda and Sharp (1950) consider its distribution to represent that of the vegetation types in which most of these disjuncts occur.

HAMAMELIS VIRGINIANA L. (Map 4).

PRUNUS SEROTINA Ehrh.: This species has recently been studied and mapped by McVaugh (1951, 1952). Three taxa, subspecies *serotina*, *hirsuta* and *eximia*, are of special interest to the present paper. The subspecies *hirsuta* (Ell.) McVaugh is a primitive, conservative population of the southeastern United States, which is now hybridizing with the subspecies *serotina*. Though McVaugh thinks that the original isolation of subsp. *hirsuta* probably dates back to the Cretaceous, it is possible that it dates only to the early Pleistocene. The subsp. *serotina* is a wide-ranging and more aggressive type occurring in much of the eastern United States, Mexico and Guatemala. McVaugh feels that it may have spread northward into the United States in the Pleistocene. It shows evidences of introgression from subsp. *hirsuta* in much of its range. Subsp. *eximia*, of central Texas, appears to be a recent offshoot of subsp. *serotina* which was separated from that population without being affected by introgression from subsp. *hirsuta*. It may be that the migrations of the Pleistocene brought about hybridization which was important in the formation of the modern subspecies *serotina*.

NYSSA SYLVATICA Marsh (Map 5).

CORNUS FLORIDA L. & var. URBINIANA (Rose) Wang (Map 6).

SIMILAR FAUNISTIC RELATIONSHIPS

It might be expected that some animal species or genera would show similar patterns, but relatively few examples are available. Epling (Dobzhansky & Epling, 1944) has attempted

to correlate the occurrence of a chromosome inversion phylad of *Drosophila pseudoobscura* in Mexico and Guatemala with the distribution of the Arcto-Tertiary forest species which occur in this region. However, this species of *Drosophila* is not present in the eastern United States, and its range in the western United States is scarcely to be correlated with the Arcto-Tertiary forest type.

Schmidt (1946) has noted the relationships between Central America and eastern North America in their herpetological faunas. In a general way this relationship parallels the floristic pattern, but it is largely on the generic rather than the species level, and it may well be an older pattern.

THE PATTERN OF DISTRIBUTION

Our knowledge of the east Mexican flora seems too inadequate to warrant an attempt at mathematical treatment of the types of distribution and plants involved. It is clear, however, that many plants are distributed in the way indicated and that many of the ranges are disjunct. It is interesting to compare these disjunctions with those involving southeastern United States and eastern Asia, since a number of the same genera are involved in both relationships (Gray, 1859; Li, 1952). The most striking difference is that the Mexican plants, unlike the Asiatic ones, are frequently the same species as those in the United States. In some cases varieties have been recognized and sometimes questionable species, but many are clearly the same species in both areas. While many of the Mexican disjuncts are trees, a number are herbaceous plants, including at least one grass. The herbaceous flora is probably less strictly bound by vegetational limits and therefore less likely to be disjunct. In addition, the herbs are less well known, because nothing comparable to Standley's *Trees and Shrubs of Mexico* is available to aid in their study. It appears, however, that the peculiar herbaceous endemics of the southeastern United States and of that area and Asia (such as the several Berberidaceous herbs listed by Li, 1952) are absent from Mexico. This may be due to the generally tropical nature of the undergrowth, even where the dominants are temperate species (Miranda & Sharp, 1950; Leopold, 1950). This feature would also reduce the probability of faunistic parallels.

The areas south of the United States where the greatest number of these plants occur are between Zacualtipán, Hidalgo and Jalapa, Veracruz, about the Mesa de San Cristóbal, Chiapas and in the mountains of Guatemala. In all these areas the plants occur most frequently on mountain escarpments, where locally temperate climate with adequate rainfall may be found. That rainfall is probably the most critical factor in accounting for the present disjunction of these species is seen by referring to the vegetation and rainfall maps for this area (Maps 7 & 8). These plants are largely coincident with the more mesic forest types. These forests, in the region of discontinuity, correspond roughly with the areas receiving over forty inches of rainfall annually. Farther south a higher rainfall figure, 50 or 60 inches, corresponds more closely to the vegetational pattern.

An interesting parallel to this distribution pattern is to be found in southeastern Asia, where Li (1952, p. 402) notes of these temperate genera: "Some genera also extend into the tropical regions of Asia, to Malaysia, . . . But in these warmer regions they represent only rare relic elements, inhabiting mostly the mountain regions." The faunistic relationships are also generally parallel in the two areas (Schmidt, 1946).

OTHER EXTRA-TROPICAL RELATIONSHIPS OF THE MEXICAN FLORA

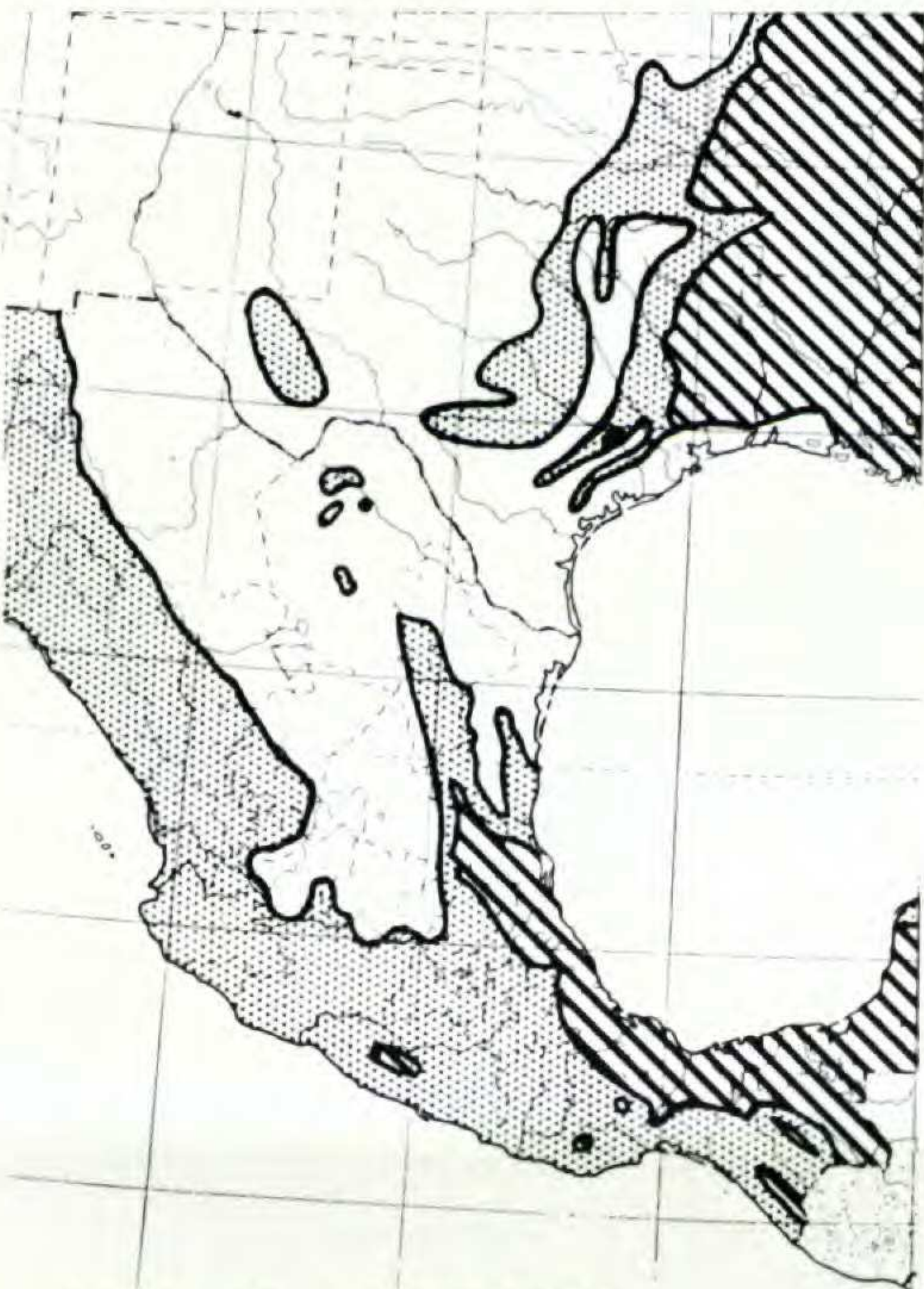
Miranda and Sharp (1950) point out several plants of the eastern escarpment which seem to be conspecific with, or closely related to, West Indian species; these may represent a dissected circum-Caribbean pattern of distribution. The other floristic element of the east Mexican flora which must be considered here is that which it shares with the western United States and northwestern Mexico. Miranda and Sharp (1950) observe that the floristic dissimilarity between eastern and western United States seems to extend into Mexico but with diminished intensity. However, as they note, a west-American element is conspicuous in eastern Mexico. Muller (1947) draws attention to the close relationships between the chaparral vegetation of northeastern Mexico and that of California. The two-fold relationship between the Mexican and the United States floras extends south into Guatemala, where Steyermark (1950) notes,



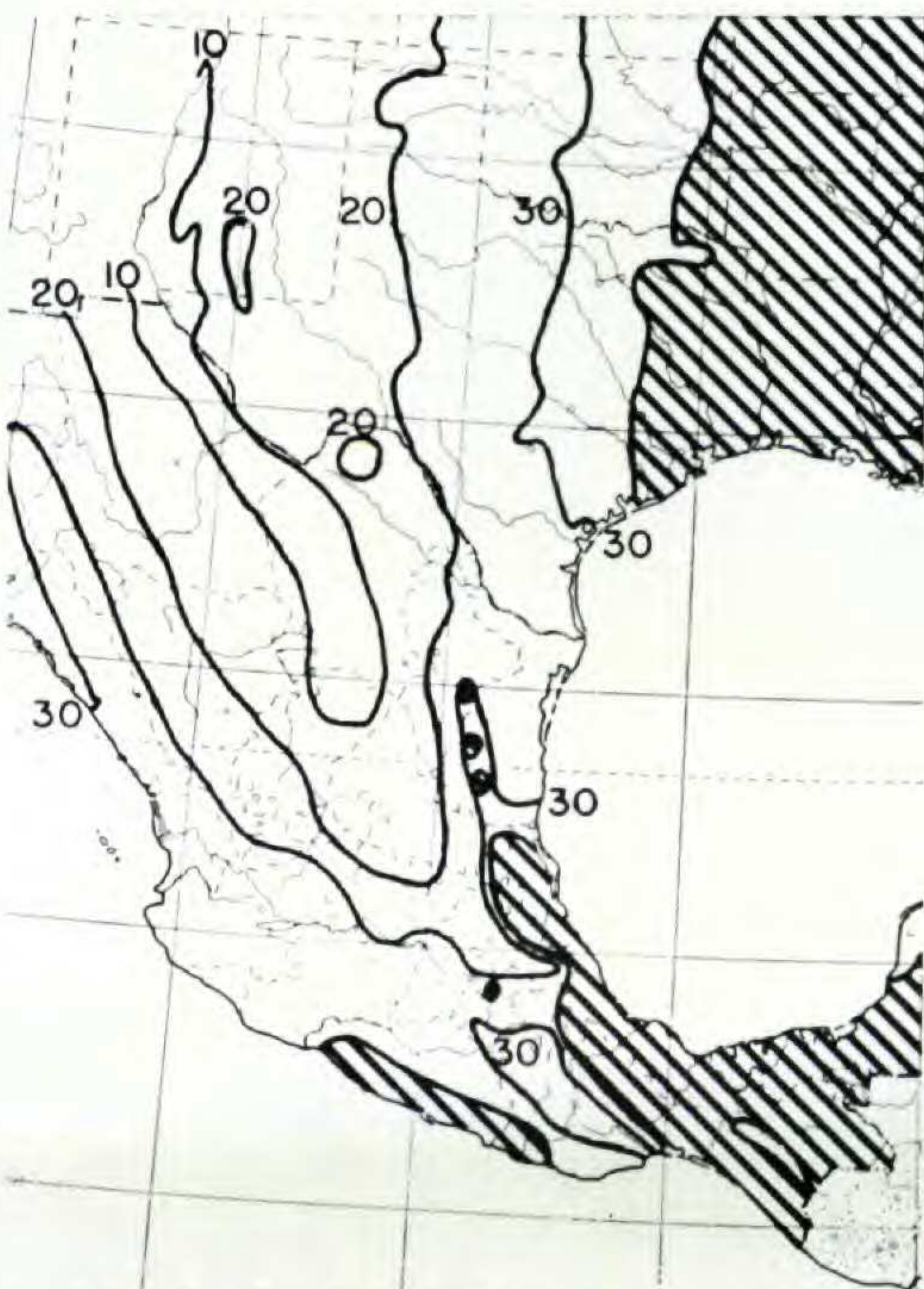
MAP 5. NYSSA



MAP 6. CORNUS



MAP 7. FORESTS



MAP 8. RAINFALL

MAP 5. *Nyssa sylvatica*. Data from Miranda (1945) and Munns (1938). MAP 6. *Cornus florida*. Data from Munns (1938) and Rickett (1950). MAP 7. Forest distribution in Texas and eastern Mexico. Diagonal lines represent mesophytic forest types, while the stippled area represents xerophytic forest types. Adapted from Braun (1950), Leopold (1950) and Tharp (1939). MAP 8. Annual rainfall distribution in Texas and eastern Mexico. Diagonal lines represent areas receiving 40 inches or more of rainfall annually. Adapted from Brooks, et al (1936), Shreve (1944) and U.S.D.A. Yearbook, 1941.

in addition to the eastern types, a strong element with its affinities in the Rocky Mountain area, including such genera as *Calochortus*, *Zygadenus*, *Montia*, *Gaura* and *Penstemon*. The elements involved in this relationship are Madro-Tertiary or Cordilleran (Axelrod, 1939) rather than Arcto-Tertiary as are the eastern disjuncts. The noteworthy feature of the western relationships is that the Mexican and Guatemalan plants are rather consistently different species than those of the western United States, a fact which may be of some value in interpreting these relationships.

HISTORICAL INTERPRETATION

Before attempting to present a coherent explanation of these relationships, it seems most convenient to review and discuss briefly the various explanations which have been offered.

Epling (Dobzhansky & Epling, 1944), in his discussion of *Drosophila*, attempts to correlate the distribution of a *Drosophila* phylad with that of the Arcto-Tertiary forest, and thus with many of the plant disjuncts considered here. His interpretation of past forest distributions is perhaps the earliest to give much attention to the Mexican-Guatemalan outliers of northern types, and is in keeping with previous vague suggestions implying an early Tertiary age for this floristic relationship. He concludes that the present distribution of *Drosophila* must have arisen either in the pluvial periods of the Pleistocene or in the early Tertiary and strongly favors the latter on paleobotanical and paleoclimatic grounds. His conclusions concerning *Drosophila* have proven controversial and have been discussed at length elsewhere (Mayr, et al. 1945). In any case, the disjunction in *Drosophila* does not parallel that in the forest species with which it is associated in southern Mexico and Guatemala.

Steyermark (1950) notes the two-fold floristic relationship between Guatemala and the United States and considers the relationship with eastern North America to be the more ancient. Following concepts developed by Fernald (1931) and Braun (1947, 1950), he notes that the area occupied by these types in Guatemala includes the oldest land surfaces in the country and that these same plants occupy the Ozarkian and Appalachian plateaus, also old land surfaces. Steyermark concludes that

these northern plants occupied both the Appalachian region and the Guatemalan highlands in the early Tertiary when these areas were reduced to low-lying peneplains. He observes that many of these plants occur in the North American Coastal Plain flora, but does not explain the failure of these species to migrate to younger land surfaces in Central America. It would appear that the occurrence of these plants in the latitude of Guatemala is dependent upon the effects of altitude; if this be the case, they could not have existed there when the area was peneplained. The relationships between Guatemala and western North America seem, on the basis of geological and floristic evidence, to be older than the eastern relationships. Steyermark's explanation of the floristic differences between eastern and western North America as being due to the Cretaceous seas seems equally doubtful in view of the evidence from paleobotany that these differences have largely been of more recent origin.

McVaugh (1952) thinks it probable that many of these temperate types may have persisted in Mexico and Central America since the early Tertiary or even the Cretaceous, and stresses the occurrence of temperate and tropical types in the same area at different altitudes. It is the dependence of these temperate types on higher altitudes which weakens the argument. It seems improbable that these temperate types could have persisted in Mexico in the early Tertiary when the climatic-vegetational zones were much farther north than now and mountain ranges were poorly developed. While I do not doubt the ultimately tropical origins of many groups, those populations which are conspecific in Central America and temperate North America would seem to have had, as suggested by Miranda and Sharp (1950), "a northern evolution and relationship", at least during the Tertiary. McVaugh's plea for a consideration of the whole of North America in botanical studies is laudable, and the phylogenetic pattern which he offers is probably quite applicable to many plants, especially the more modern herbs, such as *Lobelia* and *Salvia*.

Gentry (1946, p. 461), in describing a similar but less striking mixture of tropical and temperate types in western Mexico, states: "Most of such distributions appear to be relics repre-

senting Pleistocene adventives established during glacial epochs, when the cold front was farther south." This is an explanation which must be given due consideration, and, as will be shown, there is considerable evidence in its favor.

Deevey (1949), though not directly concerned with the present problem, stresses the importance of the Pleistocene in shaping modern ranges and suggests that temperate species were "pushed south of the Rio Grande" during parts of the Pleistocene. While it seems, as Deevey admits, that "southeastern North America taken as a whole may have served as a refuge," great distributional changes must have taken place during the Pleistocene, and these changes are probably directly related to the present problem. Deevey stresses the necessity of studying Mexico and other non-glaciated areas to a proper understanding of the Pleistocene.

Sharp (1951) draws attention to the close generic parallels between the Eocene Wilcox flora and the modern flora of the Mexican eastern escarpments. More genera (68%) of the Wilcox flora are represented in eastern Mexico than in any other area. It is noted that there are a few more temperate types represented in the Wilcox strata than Berry (1937) had thought. Sharp feels that, barring extensive parallel changes in ecological requirements, such a mixture of "temperate" and "tropical" types demands either transport from the uplands or greater ecological amplitude for many genera in the early Tertiary, and favors the latter explanation. Brown (1946), however, implies that long distance transport may have been involved in the case of some of these temperate types. There remains the possibility that a lessening of the climatic extremes might allow such a seemingly incongruous mixture of floristic types (Axelrod, 1948). Many of the east Mexican disjuncts probably occurred in Eocene time further north than the Wilcox area, and perhaps at higher altitudes.

In a more recent paper, (1953), Sharp reviews the floristic relationships between Mexico and other parts of the world and points out the fact that the physiographic history of Mexico seems to indicate a relatively recent invasion from the north for temperate types.

GEOLOGICAL AND PALEOBOTANICAL EVIDENCE

If, as appears to be the case, the presence of most "temperate" species in tropical latitudes is dependent upon high altitude habitats, then the physiographic history of southern North America is a critical part of the evidence. The material for the following summary was largely obtained from Garfias and Chapin (1949). While some mountain building occurred at about the close of the Cretaceous, the effects of this orogeny were largely nullified by early Tertiary peneplanation, this apparently culminating in the low relief of the Oligocene. Thus, for our purposes, the history of the present Mexican mountains may begin in the Miocene. The Sierra Madre Occidental arose at this time and the Sierra Madre del Sur also underwent some uplift, so that a mountain chain traversing western North America was available from the Miocene onward. The physiographic ties binding Mexico and Central America to the western United States seem to have been stronger than those connecting to the eastern United States, at least in the Cretaceous and earlier Tertiary. The western mountains, however, are not involved in the distribution of the majority of the temperate, Arcto-Tertiary disjuncts. The Sierra Madre Oriental, the critical link in these distributions, was not uplifted until the Pliocene. Since its uplift, the northern part of this mountain range has undergone considerable erosion, reaching a mature stage, with the mountains now somewhat discontinuous in the north. This would point to the late Pliocene or earlier Pleistocene as the time most favorable, physiographically, for the development of the ranges with which we are here concerned. The Sierra Madre del Sur was further uplifted in the Pliocene and the Sierra de Chiapas and related mountains of Guatemala were greatly uplifted in the late Pliocene.

The paleobotanical evidence is almost non-existent for critical areas, but gives climatic and floristic evidence for other areas, which can be correlated with the physiographic evidence to give a tentative interpretation. As previously stated, it seems improbable that a significant number of temperate plants could have persisted in Mexico during the Eocene or Oligocene. The first montane connections with temperate North America, in the Miocene, were with the western United States. The relative

absence of Arcto-Tertiary types from western Mexico argues that the area of the xeric Madro-Tertiary flora in northwestern Mexico was an effective barrier to the Arcto-Tertiary types or that climatic conditions were not then such as to push them that far south. The prairie vegetation was already developing in the central United States (Chaney & Elias, 1936; Elias, 1942) at this time, and North America was being effectively divided into eastern and western floristic areas. The movement of Cordilleran and Madro-Tertiary elements southward toward Guatemala was probably underway at this time.

During the Pliocene physiographic connections between the eastern United States and Mexico developed, but the middle Pliocene, at least, appears to have been a period of aridity (Axelrod, 1948), scarcely the proper setting for the southward extension of mesophytic plants. This was probably the time of the maximum extension of Madro-Tertiary plants, including the western types in northeastern Mexico (Miranda & Sharp, 1950, Muller, 1947), in Guatemala (Steyermark, 1950) and in the southeastern United States (McVaugh, 1943). Again, paleobotanical data for the critical areas are few, but the Clarendon florule from northern Texas exhibits Madro-Tertiary species of an aspect more xeric than that of the floras farther north (Axelrod, 1948; Chaney & Elias, 1936).

It is in the Pleistocene that the proper climatic and physiographic conditions for a floristic exchange between eastern Mexico and the eastern United States seem to be met. It is difficult to localize these contacts in the Pleistocene. The physiographic evidence points to but does not require an earlier Pleistocene time. The latest that this vegetation could have been continuous would be before the xerothermic period (if it was felt, as such, in that region), though the disjunction may have arisen at an earlier time. Evidence from pollen analysis indicates that east Texas had a cooler and more mesic climate in the past (Pötzger & Tharp, 1947) and shows a long period of climatic fluctuation for Mexico (Sears & Clisby, 1952). If the Pleistocene was felt by marked pluvial periods in the southwest, the relative absence of mesic disjuncts in western Mexico is probably to be explained by the Pliocene modernization of the western United States (Axelrod, 1948). Few mesic

plants were available in the western United States by Pleistocene time.

The floristic data support the interpretation here given in that many of the most striking eastern disjuncts have not developed into separate species, while the Mexican and Guatemalan plants with relatives in the western United States are usually distinct species. Evidence of this nature cannot be precise, but its general utility has been pointed out by Fernald (1931) and Li (1952). Particularly interesting are *Carya*, *Magnolia*, *Hamamelis*, *Liquidambar*, *Cercis*, *Parthenocissus*, *Nyssa* and *Mitchella*. All of these genera have distinct species in eastern Asia and the southeastern United States, but the Mexican and Guatemalan plants are, in each case, conspecific with those of the United States. Schmidt's zoogeographic paper (1946) deserves mention, and the chart on page 151, though not directly applicable to this problem, deserves the attention of phytogeographers. The faunistic evidence generally parallels that available from plant geography.

The main vegetational continuity in the east probably occurred not through the most direct route now available but through the Big Bend region, being determined by physiography. The present xeric forest types are nearly continuous along this route (see Map 7). This area is also of interest in that it has been suggested as the path along which an aboriginal culture pattern including agriculture with maize, beans and perhaps squash entered the United States (Thone, 1935). More data from pollen analysis is greatly to be desired from this region.

SUMMARY

The importance of Mexico to North American biogeography is noted and the two-fold relationship between Mexico and the eastern and western United States is discussed. Some species involved in the Guatemala and eastern Mexico-southeastern United States pattern of distribution are discussed and a few are mapped. The physiographic and paleobotanical evidence is reviewed and it is concluded that temperate types may have migrated southward in western North America as early as the Miocene. The western temperate groups in Guatemala may well have arrived there, as Steyermark suggests, in the Pliocene.

The eastern North American plants, on the other hand, probably did not migrate southward into Mexico and Guatemala until the early Pleistocene. These eastern species have since become disjunct because of decreased rainfall in Texas and northeastern Mexico.

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